Yousuf A. Khan

Stanford University

Ph.D. (B.S., M.Phil., M.S.)

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Educational and Professional Experiences

2019 – 2025**: Stanford University** – Ph.D. in Molecular and Cellular Physiology. Thesis Topic: *The structural and functional principles of SNARE disassembly by the AAA+ complex, Sec18/NSF* (GPA: 4.1/4.0).

2023–2024: **EvolutionaryScale:** Research Scientist Intern on Artificial Intelligence for Science. Project: *Using language models to simulate 500 million years of evolution*

2022 –2022: **Google DeepMind**: Research Scientist Intern on AlphaFold team. Project: *Applying Deep Learning to predicting macromolecular structures*

2020 – 2023: **Stanford University** – M.S. in Biomedical Informatics. Selected coursework: *Design and Analysis of Algorithms, Applied Machine Learning, Modern Applied Statistics: Supervised Learning, Representations and Algorithms for Computational Molecular Biology* (GPA: 4.1/4.0)

2018 – 2019: **University of Cambridge** - Masters of Philosophy in Biological Sciences (Pathology). Thesis: *Examining Programmed −1 Ribosomal Frameshifting in Homo sapiens*

2014 – 2018: **University of Maryland, College Park** Bachelors of Science in Cellular Biology and Molecular Genetics (Summa Cum Laude, GPA: 4.0/4.0, High Honors). Thesis: *Reactive Oxygen Species signaling in Leishmania species*

Selected Awards and Honors

2024 MCP Student Spotlight Speaker, Stanford University

2024 Oral Presentation, EMBO Recoding Conference (Cork, Ireland)

2023 NIH F31 Ruth L. Kirschstein Predoctoral Individual National Research Service Award

2023 Travel Grant Awardee (Oral Presentation), EMBO Membrane Fusion Conference (Göttingen, Germany)

2019 Knight-Hennessy Fellowship

2019 NSF Graduate Research Fellowship

2019 Best Student Poster Award, Ribosome Conference (Merida, Mexico)

2019 National Science Foundation Travel Fellowship, Ribosome Conference (Merida, Mexico)

2018 Winston Churchill Scholarship to the University of Cambridge

2018 J. Howard Brown Award for best student abstract, American Society for Microbiology

2018 Honors Citation from Integrated Life Sciences Program, University of Maryland

2017 Howard Hughes Medical Institute Undergraduate Research Fellowship

2016 Barry M. Goldwater Scholarship

2016 Dr. Laffer Scholarship for Excellence in Research

2015 – 2016 Maryland Summer Scholars Research Fellowship

2014 – 2018 Dean's List, University of Maryland

2014 Full Banneker/Key scholarship, University of Maryland

Manuscripts: 8 (co*)First and (co#)Corresponding Authorship

1. Synaptobrevin-2 Disease Variants Reveal Spatial Constraints Within the Presynaptic Active Zone. Guzikowski NJ, Shin O, **Khan YA**, Esquivies L, Alten B, Brunger AT and Kavalali ET. ***Under text revision at PNAS***.

2. In-Situ Structure and Topography of AMPA Receptor Scaffolding Complexes Visualized by CryoET. Held RG, Liang J, Esquivies L, **Khan YA**, Wang C, Azubel M, Brunger AT. ***Under review at Science*** (bioRxiv: https://doi.org/10.1101/2024.10.19.619226)

3. SNARE disassembly requires Sec18/NSF side loading. **#Khan YA**, White KI, Pfuetzner RA, Singal B, Esquivis L, Mckenzie G, Liu F, DeLong K, Choi UB, Montabana E, Mclaughlin T, Wickner WT, #Brunger AT. **Nature Structural and Molecular Biology**. 2025 Jul 2. doi: 10.1038/s41594-025-01590-w

4. Programmed ribosomal frameshifting during PLEKHM2 mRNA decoding generates a constitutively active mediator of kinesin-1-dependent lysosome transport. Loughran G**,** De Pace R, Carancini G, Mudge MJ, Kellis M, Atkins JF, Baranov PV, Firth AE, Bonifacino JS, **#Khan YA**. ***Under review at Science Advances*** (bioRxiv: https://doi.org/10.1101/2024.08.30.610563)

5. NSF converts syntaxin nanodomains to a priming-ready state. White KI, **Khan YA**, Qiu K, Couoh-Cardel S, Esquivies L, Pfuetzner R, Diao J, Brunger AT. ***Accepted and in press at Nature Communications.*** (bioRxiv: https://doi.org/10.1101/2024.10.11.617886)

6. Simulating 500 million years of evolution with a language model. Hayes T, …, **Khan YA**, … Rives A. **Science**. 2025 Jan 16:eads0018. doi: 10.1126/science.ads0018.

7. Abramson J, .., **Khan YA**, …, Hassabis D, Jumper JM. Accurate structure prediction of biomolecular interactions with AlphaFold 3. **Nature**. 2024 Jun;630(8016):493-500. doi: 10.1038/s41586-024-07487-w.

8. **#Khan YA,** Hokia C, Xu J, Ehlert B. covLLM: Large Language Models for COVID-19 Biomedical Literature. **arXiv**. 2023 https://doi.org/10.48550/arXiv.2306.04926.

9. *Gao Y, ***Khan YA**, Mo W, White KI, Perkins M, Pfuetzner RA, Trapani JG, Brunger AT, Nicolson T. Sensory deficit screen identifies nsf mutation that differentially affects SNARE recycling and quality control. **Cell Rep**. 2023 Apr 5;42(4):112345. doi: 10.1016/j.celrep.2023.112345.

10. Loughran G., Fedorova A. D., **Khan YA**, Atkins J. F., & Baranov P. V. (2022). Lack of evidence for ribosomal frameshifting in ATP7B mRNA decoding. **Molecular cell**, *82*(19), 3745-3749.

11. ***Khan YA**, *Loughran G, Steckelberg AL, Brown K, Kiniry SJ, Stewart H, Baranov PV, Kieft JS, Firth AE, Atkins JF. Evaluating ribosomal frameshifting in CCR5 mRNA decoding. **Nature**. 2022 Apr;604(7906):E16-E23. doi: 10.1038/s41586-022-04627-y.

12. Zhang K, Horikoshi N, Li S, Powers AS, Hameedi MA, Pintilie GD, Chae HD, **Khan YA**, Suomivuori CM, Dror RO, Sakamoto KM, Chiu W, Wakatsuki S. Cryo-EM, Protein Engineering, and Simulation Enable the Development

of Peptide Therapeutics against Acute Myeloid Leukemia. **ACS Cent Sci**. 2022 Feb 23;8(2):214-222. doi: 10.1021/acscentsci.1c01090. Epub 2022 Feb 7.

13. **#Khan YA**, White KI, #Brunger AT. The AAA+ superfamily: a review of the structural and mechanistic principles of these molecular machines. **Crit Rev Biochem Mol Biol**. 2022 Apr;57(2):156-187. doi: 10.1080/10409238.2021.1979460. Epub 2021 Oct 11.

14. **#Khan YA**, #Jungreis I, Wright JC, Mudge JM, Choudhary JS, Firth AE, Kellis M. Evidence for a novel overlapping coding sequence in POLG initiated at a CUG start codon. **BMC Genetics**. 2020;21(1):25. Published 2020 Mar 6. doi:10.1186/s12863-020-0828-7

15. Rocco-Machado N, Cosentino-Gomes D, Nascimento M, L. Paes Vieriera, **Khan YA**, Mittra B, Andrews NW, Meyer-Fernandes JR. Leishmania amazonensis ferric iron reductase (LFR1) is a bifunctional enzyme: Unveiling a NADPH oxidase activity. **Free Radical Biology and Medicine**. 2019;143:341-353. doi:10.1016/j.freeradbiomed.2019.08.026.

16. **Khan YA**, Andrews NW, Mittra B. ROS regulate differentiation of visceralizing Leishmania species into the virulent amastigote form. **Parasitology Open**. 2018;4:e19. doi:10.1017/pao.2018.15

17. Sarkar A, **Khan YA**, Laranjeira-Silva MF, Andrews NW, Mittra B. Quantification of Intracellular Growth Inside Macrophages is a Fast and Reliable Method for Assessing the Virulence of Leishmania Parasites. **Journal of Visualized Experiments**. 2018;(133):57486. Published 2018 Mar 16. doi:10.3791/57486

18. Briggs JW, Ren L, Chakrabarti KR, Tsai YC, Weissman AM, Hansen RJ, Gustafson DL, **Khan YA**, Dinman JD, Khanna C. Activation of the unfolded protein response in sarcoma cells treated with rapamycin or temsirolimus. **PLoS One**. 2017;12(9):e0185089. Published 2017 Sep 19. doi:10.1371/journal.pone.0185089

19. Girardi T, Vereecke S, Sulima SO, **Khan Y**, Fancello L, Briggs JW, Schwab C, de Beeck JO, Verbeeck J, Royaert J, Geerdens E, Vicente C, Bornschein S, Harrison CJ, Meijerink JP, Cools J, Dinman JD, Kampen KR, De Keersmaecker K. The T-cell leukemia-associated ribosomal RPL10 R98S mutation enhances JAK-STAT signaling. **Leukemia.** 2018;32(3):809–819. doi:10.1038/leu.2017.225

20. Meydan S, Klepacki D, Karthikeyan S, Margus T, Thomas P, Jones JE, **Khan Y**, Briggs J, Dinman JD, Vázquez-Laslop N, Mankin AS. Programmed Ribosomal Frameshifting Generates a Copper Transporter and a Copper Chaperone from the Same Gene. **Molecular Cell**. 2017;65(2):207–219. doi:10.1016/j.molcel.2016.12.008

21. Kendra JA, de la Fuente C, Brahms A, Woodson C, Bell TM, Chen B, **Khan YA**, Jacobs JL, Kehn-Hall K, Dinman JD. Ablation of Programmed -1 Ribosomal Frameshifting in Venezuelan Equine Encephalitis Virus Results in Attenuated Neuropathogenicity. **Journal of Virology**. 2017;91(3):e01766-16. Published 2017 Jan 18. doi:10.1128/JVI.01766-16

22. Moomau C, Musalgaonkar S, **Khan YA**, Jones JE, Dinman JD. Structural and Functional Characterization of Programmed Ribosomal Frameshift Signals in West Nile Virus Strains Reveals High Structural Plasticity Among cis-Acting RNA Elements. **Journal of Biological Chemistry**. 2016;291(30):15788–15795. doi:10.1074/jbc.M116.735613